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Tamias palmeri. By Troy L. Best

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Tamias palmeri (Merriam, 1897)

Palmer's Chipmunk

Eutamias palmeri Merriam, 1897:208. Type locality "Charleston Peak [Clark Co.—Miller, 1924:205], Nevada (altitude about 2450 meters or 8000 feet)."

Tamias palmeri Elliot, 1901:69. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains ca. 25 species (Honacki et al., 1982; Patterson, 1984). *T. palmeri* (Fig. 1) is in the subgenus *Neotamias* (Levenson et al., 1985). *T. palmeri* is monotypic (Hall, 1981).

DIAGNOSIS. The only species of *Tamias* sympatric with *T. palmeri* is *T. panamintinus*. From *T. panamintinus*, *T. palmeri* differs in greater size, grayer shoulders, more solidly black and solidly white dorsal stripes (Hall, 1946), more tawny coloration of the body, much paler ventral surface of the tail (Burt, 1934), narrower and less-flattened braincase, longer upper incisors, larger cheekteeth, and more nearly parallel zygomatic arches (Fig. 2; Hall, 1946).

From nearby populations of its closest relative, T. umbrinus, T. palmeri differs in having browner (more reddish) dark dorsal stripes, more tawny color on the underside of the tail, shorter rostrum, and shorter upper incisors (Hall, 1946, 1981). T. palmeri and T. umbrinus have similar karyotypes (Sutton and Nadler, 1969) and phalli, but the baculum of T. palmeri is relatively distinct from that of T. umbrinus; T. palmeri has a less acute angle between the tip and shaft (average, 114.8° compared with 120.5-124.3° in three populations of T. umbrinus) and greater height of shaft (average, 0.86 mm compared with 0.65-0.76 mm in three populations of T. umbrinus—Stanley, 1991). Intergradation does not occur between these two species because deserts, inhospitable to chipmunks, isolate T. palmeri from T. umbrinus (White, 1953).

GENERAL CHARACTERS. In Nevada, differences between coloration of winter and summer pelage are greater in T.



Fig. 1. A young *Tamias palmeri* in Kyle Canyon, Mt. Charleston, Spring Mountains, Clark Co., Nevada. Photograph courtesy of H. E. Broadbooks.

palmeri than in T. umbrinus inyoensis, T. umbrinus nevadensis, or T. speciosus frater (Hall, 1946). In summer pelage (early July), the sides of the nose of T. palmeri are pale pinkish-cinnamon, and the top of the head is smoke gray mixed with pale pinkish-cinnamon



Fig. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias palmeri* from Charleston Park on Charleston Peak, 2,400 m elev., Clark Co., Nevada (male, Museum of Vertebrate Zoology, University of California, Berkeley 151318). Greatest length of cranium is 35.5 mm. Photographs by T. H. Henry.

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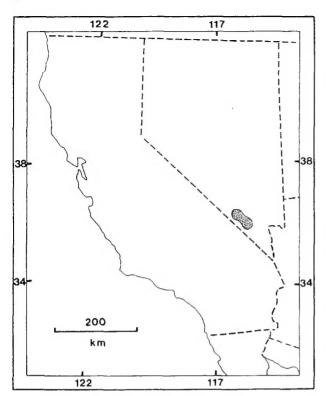


Fig. 3. Distribution of *Tamias palmeri* in Nevada (Hall, 1981).

and bordered on the sides of the crown with fuscous. The facial stripes are sayal brown, shaded with fuscous, and the median stripe has some fuscous black in front of and behind the eye. The ears are sayal brown anteriorly, buffy white posteriorly, and clouded with fuscous medially. The postauricular patches (posterior to ear) are grayish white or creamy white. The median dorsal stripe is narrow, fuscous black, and bordered with mikado brown. The outer pair of dark stripes is mikado brown and shaded with fuscous. The median pair of pale stripes is pale smoke-gray and the outer pair is creamy white. There are no outer stripes. The sides are tawny or cinnamon, shading to pale russet. The rump and thighs are cinnamon buff, shaded with fuscous and smoke gray. The feet are pinkish buff or pinkish cinnamon. Dorsally, the tail is fuscous black (the bases of the hairs are cinnamon) and it is edged with pinkish buff. Ventrally, the tail is ochraceous tawny and bordered with fuscous black and edged with pinkish buff. The underparts are creamy white (color nomenclature follows Ridgway, 1912—Howell, 1929).

In winter pelage (February), the upperparts are grayer than in summer and the dark dorsal stripes are less distinct. The sides of the nose are clay colored. The dark dorsal stripes are sayal brown, and the median one is fuscous black in the center. The pale dorsal stripes are pale smoke-gray, and the outer pair is more whitish. The nape and shoulders are washed with pale smoke-gray. The rump and thighs are smoke gray and washed with cinnamon buff. The sides are sayal brown, shading to cinnamon buff on the sides of the neck. The feet and tail are the same color as in summer pelage (Howell, 1929).

As in all members of the subgenus Neotamias, the dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Hall, 1946; Howell, 1929). There is no significant sexual dimorphism in size (Hirshfeld and Bradley, 1977; Levenson, 1990). Average and range of measurements (in mm) of sexes combined are: total length, 220 (210-223); length of tail, 94.6 (86.5-101.0); length of hind foot, 33.1 (32.5-34.0); length of ear from notch, 14.6 (13.5-15.5); greatest length of cranium, 35.9 (34.9-36.5); zygomatic breadth, 19.6 (19.1-19.9); cranial breadth, 15.4 (15.1-15.8); interorbital breadth, 8.3 (8.0-8.8); length of nasals, 11.3 (10.7-12.0—Howell, 1929).

Estimates of mass range from 50.0 to 69.4 g (Gannon and Stanley, 1991; Hall, 1946; Scott et al., 1972, 1976; Yousef et al., 1974). Males attain greatest mass during April and May, with a

decrease through summer months. Females attain greatest mass in July (Hirshfeld, 1975).

DISTRIBUTION. Palmer's chipmunk is endemic to the Spring Mountains, Clark Co., Nevada (Fig. 3); it occurs at 2,100-3,600 m elev. (Burt, 1934), but is most abundant at 2,400-2,550 m elev. (Deacon et al., 1964). The Spring Mountains are surrounded by deserts, which limit the distribution of *T. palmeri* (Merriam, 1897).

FOSSIL RECORD. Tamias evolved by the early Miocene (Black, 1972). Reconstruction of the ranges of T. palmeri, T. quadrimaculatus, and T. umbrinus at the height of the last glaciation reveals that they were in contact. T. palmeri probably diverged from T. umbrinus during a period of interglacial isolation in a montane coniferous forest refugium similar to the one T. palmeri now inhabits (Hoffmann, 1981). No fossils of T. palmeri are known.

FORM AND FUNCTION. Adult males molt from winter to summer pelage during May and June, and from summer to winter pelage during late August, September, and October. Progression of molt is from anterior to posterior in spring, and the reverse in autumn. Females molt in a similar time frame, but their molt to summer pelage primarily occurs in June and July. Although this 1-month delay may reflect the metabolic burden of pregnancy and lactation, one female that gave birth in the laboratory in June was molting during lactation (Hirshfeld, 1975). In some Palmer's chipmunks, the molt progresses in a definite line, whereas in others it is irregular over the body. Some from 2,400 m elev. had molted in early June, whereas a male from 3,510 m elev. had worn winter pelage on 4 July, except for a small area on his head (Burt, 1934).

Average and range of mass of organs (in g/kg) are: brain, 36.4 (30.2-40.2); heart, 5.2 (3.7-6.6); kidney, 9.5 (7.2-11.1); liver, 33.3 (20.6-54.5); lung, 14.3 (11.8-16.7); pancreas, 4.0 (2.8-5.1); adrenals, 0.47 (0.27-0.87); adrenals of breeding males, 0.56 (0.39-0.98); adrenals of non-breeding males, 0.05 (0.01-0.10); testes of breeding males, 8.6 (4.5-14.7); testes of non-breeding males, 1.0 (0.8-1.5); ovaries, 1.6 (0.5-2.1). Because of their larger body mass, females average larger than males in mass of organs (Hirshfeld, 1975). At an average body mass of 65 g, fatfree body mass averages 55.7 g (Scott et al., 1972).

The minimal rate of metabolism, expressed as a measure of the volume of oxygen consumed, is 1.45-1.63 ml of oxygen g⁻¹ h⁻¹ (Scott et al., 1972; Yousef et al., 1974). The amount of thyroxine in the blood plasma (58 ng/ml) is related to basal metabolism and ecologic distribution (Scott et al., 1976).

Data on the relationship between ambient temperature (°C) and average frequency of respiration (respirations/min), respectively, are: 5, 96; 10, 146; 15, 175; 20, 182; 25, 188; 30, 152; 35, 223; 40, 334. Thus, the average frequency of respiration increases steadily at ambient temperatures of 5-25°C, and then drops at 30°C when the thermoneutral zone is approached, only to rise again until the maximum frequency of respiration is attained at 40°C (Hirshfeld, 1975).

Palmer's chipmunk has a narrow thermoneutral zone (32–34°C), with a low-critical temperature of 29–32°C and a high-critical temperature of 34–36°C. Below the low-critical temperature, the volume of oxygen consumed increases linearly as ambient temperature decreases. *T. palmeri* maintains a rectal temperature of 34–36°C at ambient temperatures below the low-critical temperature; hyperthermia develops at ambient temperatures of 35–39°C. *T. palmeri* has a higher index of insulation than *T. dorsalis* and *T. minimus* (Bradley and Yousef, 1974).

The daily rectal temperature of *T. palmeri* ranges from 31.2 to 35.6°C, with a mean of 33.8°C in spring, summer, and autumn. In late autumn (November and December), the range is 28.9-33.1°C, with a mean of 31.9°C. Ambient temperatures are lowest during these 2 months (average, 20.2°C); body temperature may be related to ambient temperature or the season of the year. When active, the body temperature is higher than when inactive (Hirshfeld, 1975).

Total body water averages 48.8 ml, or 70.4 g/100 g of body mass. The turnover rate of tritiated water on a daily basis is 21.5 ml (=31.0 ml/100 g or 665 ml/kg^{0.82}). T. palmeri turns over 40% more water per unit of oxygen consumed than Neotoma lepida, Ammospermophilus leucurus, and Spermophilus lateralis (Yousef et al., 1974). Non-breeding adults consume 6-8 g of water/day and 4-5.5 g of food. They excrete ca. 4 g of urine/day and 0.6 g of feces. Breeding females consume more food and water than non-

breeding females, however, pregnant females consume more than either group. Comparisons of breeding adults and young, based upon consumption/body mass, reveal that young consume relatively greater quantities of food and water. *T. palmeri* will not readily accept water from a bottle, but it will consume whole oats and cantaloupes as a source of food and water (Hirshfeld, 1975).

When deprived of water (except for whole oats ad lib.) for 10 days, the body temperature decreased from an average of 33.8 to 29.6°C. *T. palmeri* reduced food consumption to <50% of that usually consumed after 1 day without water. Food consumption progressively declined. It appeared healthy through the 10 days, but after 5 days it often appeared asleep and was docile when handled. Upon return of the water source, original body mass was reached in 12 days (Hirshfeld, 1975).

When deprived of food (except for cantaloupes ad lib.) for 10 days, mass decreased to 91.7% of the original mass and body temperature dropped to 31.4°C. Test animals appeared normal, but generally increased consumption of water throughout the period. During the experiment, behavior appeared normal and they were still active after 10 days. However, cantaloupe was consumed at an increasing rate each day they were without food (Hirshfeld, 1975).

Average measurements (in mm) of the baculum are: length of shaft, 2.88; length of tip, 1.31; height of keel, 0.61; height of shaft, 0.86; angle between tip and shaft, 114.8°; greatest width of shaft at base, 1.16; least width of shaft at neck, 0.39; width of tip at base of keel, 0.42. Average measurements (in mm) of phallic characters are: length of urinary meatus, 0.19; width of urinary meatus, 0.38; width of lappet, 0.38 (Stanley, 1991).

Average and range of measurements (in mm) of the baubellum (os clitoris) are: length of base, 0.94 (0.72-1.10); length of shaft, 0.90 (0.85-0.98); depth of shaft, 0.47 (0.36-0.52); length of tip, 0.88 (0.78-0.98); length of keel, 0.34 (0.29-0.39); angle of the tip-shaft, 136.2° (128-142°). The baubellum of *T. palmeri* has base, shaft, and tip of nearly equal length. The base is straight, without taper and the notch between the two divergent knobs on the proximal end is ca. 0.2 mm deep. The base-shaft angle is ca. 75° and the shaft and tip are bent to the right ca. 25° from the base. The heel is a prominent knob, the keel is large, and the flanges curve along the sides of the tip to the distal end of the shaft. The side of the tip opposite the keel is concave (Sutton, 1982).

ONTOGENY AND REPRODUCTION. In late September, testes of *T. palmeri* are small (mean of 4 by 3 mm) and no embryos are present (Gamon and Stanley, 1991), but it is reproductively active from April through July. Most adult males are reproductively active (based upon testes present in the scrotum) in March-June. Timing of breeding by females and criteria for reproductive activity are less clear than for males, but copulation probably occurs in April and early May and parturition occurs in late May and June (Hirshfeld, 1975). The gestation period is at least 33 days (Hirshfeld and Bradley, 1977). Embryo counts for 15 pregnant adults were six, five (four animals), four (seven), and three (three—Deacon et al., 1964). The average number of embryos is 4.7 (range, four to seven—Hirshfeld, 1975), but the average size of four litters born in captivity was 3.8 (range, three to six—Hirshfeld and Bradley, 1977).

Half-grown young were observed at 2,400 m elev. on 6 June (Burt, 1934), 2,520 m on 21 June (Deacon et al., 1964), and 3,000 m on 9 July (Burt, 1934). Young continue to appear through August, at which time weaning apparently ends (Hirshfeld, 1975). Young are much grayer and less tawny in color than adults (Burt, 1934). Juveniles of both sexes can be distinguished from adults by smaller size of body, large head in proportion to the body, and soft, fluffy pelage (Hirshfeld, 1975).

The skin of neonates is pink and semitransparent, revealing organ movements and white areas containing milk immediately after nursing. The posterior portion of the body is darker than the anterior. Young are hairless, with the exception of the mystacial vibrissae on the sides of the nose, which appear to be ≤1 mm in length. Eyes bulge slightly and appear dark through the transparent covering of skin. The pinnae of the ears are folded tightly against the side of the head, and are ca. 1 mm in length. The toes, although distinctly formed at birth, are united by a membranous covering and possess minute claws. The young may utter faint squeaks 12–18 h after birth (Hirshfeld and Bradley, 1977), especially when the mother makes sudden movements. If separated from the mother, neonates continue suckling motions for brief periods (Hirshfeld, 1975).

Hairs and vibrissae of neonates grow rapidly. Hair on the head is visible after 10-11 days, but individual body hairs cannot be distinguished until ca. day 20. A few hairs emerge on the sides of the body by ca. day 14. A sparse growth of short hairs appears on the venter and legs on day 15. At this time, the tail is still bare, but by day 17 a few hairs appear on the proximal end. The tail is the last part of the body to acquire hair. The four pale and three dark dorsal stripes appear at 12-13 days of age. By the end of week 3, adult facial and dorsal color patterns are evident. By the end of week 4, the hair has a sleek and smooth appearance that disappears in 10-11 weeks, when young assume the general appearance of young adults (Hirshfeld and Bradley, 1977).

Grooves marking the future eye slits are noticeable within 4 days. The eyes become increasingly prominent and bulging, and open 25–26 days after birth. The pinnae of the ears, which are folded over the ear openings at birth, become erect on day 2 or 3. The external auditory meatus opens at 26–27 days. The toes begin separating at 12 days; their division is complete by day 17. The claws are clear and soft at birth. The proximal ends of the claws turn dark first, and by 3 weeks, the claws are completely dark. The lower incisors erupt at 14 days and the upper incisors appear at 21–22 days. Cheekteeth appear at 31–32 days (Hirshfeld, 1975; Hirshfeld and Bradley, 1977).

Overall activity of neonates increases during the first 48 h after birth. By 8 days, they pull themselves around by their front legs, and by 15 days they are able to hold their body off the ground. At 3 weeks, movements are jerky and uncoordinated, although they have begun to scratch their ears with the hind feet. They become active outside their nests at ca. 5 weeks of age. The young are sensitive to quick movements in their environment. By 6 weeks of age, young eat solid food and may feed as they sit on their haunches; they also clean their face in an adult manner. When asleep, young sleep with forepaws held over the face, with body and tail curled in a ball. Young raised in captivity never became accustomed to humans or to handling. During the process of catching the young, they buzzed or trilled, tried to bite, and attempted to ward off capture with the forepaws (Hirshfeld, 1975).

Average mass (in g) and external measurements (in mm) of T. palmeri at 1, 3, 5, 7, 9, 11, and 13 weeks of age, respectively, are: mass, 4.3, 9.8, 17.7, 27.7, 42.2, 50.4, 54.6; length of head and body, 44.5, 60.7, 68.0, 101.2, 111.5, 116.6, 124.2; length of tail, 14.3, 30.8, 61.0, 77.0, 79.5, 82.6, 82.6; length of hind foot, 7.8, 16.5, 25.9, 28.9, 30.2, 30.2, 30.2; length of ear, 2.0, 6.8, 13.0, 17.1, 17.8, 18.1, 18.0; length of vibrissae, 4.7, 7.5, 14.1, 18.9, 20.6, 21.1, 21.0. At 13 weeks of age, body mass is 85-90% that of adults. However, at least in the laboratory, young do not reach mass of adults by 5 months of age, whereas linear measurements attain adult proportions by ca. 13 weeks of age. That is, lengths of hind foot, tail, ear, and vibrissae reach adult size in 9-11 weeks, with length of head and body reaching adult size in 12 weeks (Hirshfeld and Bradley, 1977). T. palmeri has a greater growth-rate constant than T. panamintinus (Hirshfeld and Bradley, 1977; Levenson, 1979).

Average body temperature (°C) and oxygen consumption (ml of oxygen g⁻¹ h⁻¹), respectively, at 1, 3, 5, 7, 9, 11, and 13 weeks of age are: 26.5, 2.4; 33.5, 2.8; 34.5, 3.1; 34.5, 3.9; 35.5, 2.6; 34.5, 1.9; 34.5, 1.7 (Hirshfeld, 1975). Young attain body temperatures approaching those of adults by ca. 5 weeks of age. Rates of oxygen consumption steadily increase until ca. 8 weeks of age. Thereafter, oxygen consumption decreases progressively with age. This decrease in oxygen consumption probably is due to increase in insulation during development. Trends in oxygen consumption correspond to growth rates except during the first few weeks. At 13 weeks of age, the rate of oxygen consumption of young is ca. 85% that of adults, although at this time the young are about the size of adults. Compared with T. panamintinus, T. palmeri has a much more precocial thermoregulatory development that coincides with the accelerated ontogeny of this species (Hirshfeld and Bradley, 1976)

ECOLOGY. Tamias palmeri occurs up to timberline (ca. 3,600 m) in the Spring Mountains, Nevada, where it most often is found along rock cliffs or downed logs that afford hiding places (Burt, 1934). In Clark Canyon, Palmer's chipmunk occurs in the bristlecone pine (Pinus aristata), white fir-Ponderosa pine (Abies concolor-Pinus ponderosa), single-leaf pinyon-Utah juniper (Pinus mono-phylla-Juniperus osteosperma), and mountain mahogany-manza-

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nita (Cercocarpus ledifolius-Arctostaphylos pungens) communities. Other plants occurring in these habitats are maple (Acer glabrum), Utah serviceberry (Amelanchier utahensis), cliffrose (Purshia mexicana), shooting star (Dodecatheon redolens), mountain spray (Holodiscus dumosus), dwarf juniper (Juniperus communis), limber pine (Pinus flexilis), currant (Ribes cereum), Woods rose (Rosa woodsii), bramble (Rubus), and elderberry (Sambucus coerulea). In this canyon, Palmer's chipmunk is most abundant at elevations of 2,400–2,550 m along the floor of the canyon and lower portions of the slopes where fallen logs, large rocks, small caves, and crevices in cliffs afford shelter. It is the most abundant mammal at >2,250 m elev. (Deacon et al., 1964).

Palmer's chipmunk eats seeds, fruits, fleshy fungi, green vegetation, and insects (Yousef et al., 1974). Seeds, fruits, greens, and flowers occurred in all stomachs examined from March through September, with seeds and fruits generally greater in volume and equal in frequency to greens and flowers. Arthropods often were found, except in spring months. Small amounts of lichens, bark, and carrion also are consumed (Hirshfeld, 1975). Discarded remains of plant material beneath conifers indicate a considerable proportion of the diet consists of fruits of conifers. On 1 July, one had its cheekpouches distended with small seeds (possibly Gentianaceae—Burt, 1934). In captivity, it will eat whole oats, peanut butter, bird seed, cantaloupes, apples, lettuce, and celery (Hirshfeld and Bradley, 1977).

A tree nest of *T. palmeri* was present 60 m up the south slope of Kyle Canyon at 2,100 m elev. on 18 July. Surrounding the nest tree were mountain mahogany, small oaks (probably Gambel oak, *Quercus gambelii*), and scattered young Ponderosa pine. The tree den was in a woodpecker hole 8 m up a tall, dead, and barkless Ponderosa pine, and was serving as a den for five chipmunks. On the opposite side of the trunk was a large vertical crack (at the bottom of which was another woodpecker hole) that was a refuge, play area, and possibly an additional place to sleep (Broadbooks, 1974).

In Clark Canyon, T. palmeri primarily occurs at higher elevations than T. panamintinus, but there is broad elevational overlap. Both species occur in the white fir-Ponderosa pine (2,190-2,670 m elev.), the ecotone between pinyon-juniper and white fir-Ponderosa pine (2,460-2,520 m elev.), and the mountain mahogany-manzanita (2,280-2,460 m elev.) communities. T. palmeri is most abundant in the white fir-Ponderosa pine community and in the ecotone between the pinyon-juniper and white fir-Ponderosa pine communities, whereas T. panamintinus is most abundant in lower elevational (2,025-2,160 m) pinyon-juniper communities. Other species of small mammals occurring with T. palmeri include Ammospermophilus leucurus, Spermophilus lateralis, Perognathus parvus, Reithrodontomys megalotis, Peromyscus crinitus, P. boylii, P. maniculatus, Neotoma cinerea, and N. lepida (Deacon et al., 1964).

Internal parasites of *T. palmeri* include the acanthocephalan *Moniliformis moniliformis* and the nematodes *Syphacia eutamii*, *Heteroxynema cucullatum*, and *Pterygodermatites coloradensis* (Archie et al., 1988). The only known ectoparasite of Palmer's chipmunk is the flea *Monopsyllus eumolpi* (Hubbard, 1949).

BEHAVIOR. Palmer's chipmunk is diurnal (Scott et al., 1976), secretive, and highly mobile. It usually remains close to fallen logs and rock piles, rarely venturing away from shelter for long periods (Hirshfeld, 1975).

Tamias palmeri may become fairly tame around places of human habitation. At one summer resort, it lived beneath cabins and in piles of rock and wood (Burt, 1934). When first captured, it displays general aggressive tendencies. After some time in captivity, this tendency wanes and handling is easier. However, some males never lose their aggressiveness and will continually chatter to protect their cages from outside disturbances. Females do not act in this manner (Hirshfeld, 1975).

In captivity, females with young spend all of their time in the nesting cages. Most females appear undisturbed when young are removed from the cages, even when detached from the nipples. However, on occasion, females will leave the nest and run about the cage and then bury themselves under the nesting material. If young are attached to the nipples, this action will sometimes result in young being carried from the nest. No attempts are made by the female to carry young back to the nest, but young always are accepted when replaced (Hirshfeld, 1975).

Whether T. palmeri hibernates (Hirshfeld and Bradley, 1977) or not (O'Farrell, 1980), activity almost ceases during cold winter months. However, it may be active on snow-covered ground during December and January, when temperatures are well above normal and there are no clouds (Hirshfeld, 1975). T. palmeri was active 12–14 February when snow was on the ground; during the warm part of the day, it ran along logs and in open spaces on the sunny side of canyons (Merriam, 1897).

Males are active from March (even with 10 cm of snow on the ground) through October, with decreased activity in autumn months. Females are not active until late spring, with peak activity in mid-summer. T. palmeri appears later in spring than T. panamintinus. However, this difference in time of appearance probably is due to its occurrence at higher elevations where winters are colder and longer (Hirshfeld, 1975).

Tamias palmeri exhibits intraspecific aggression throughout the year. Physical displays of aggression are most evident in spring (Hirshfeld, 1975).

In a tree den in Kyle Canyon, a small Palmer's chipmunk and an adult were at the cervice in the den tree at 0753 h and two others that were nearby (including a juvenile) responded to squeaks emitted by a human observer. When the canyon was in deep shadows that evening at 1930 h, the mother and five young were on the den tree. The mother groomed herself, nuzzled one of her young on the nose, cheek, and shoulder, and then the two played together on the tree before all went into the nest hole between 1953 and 2008 h. No calls were heard (Broadbooks, 1974).

Types of calls (relative frequency) are the chip (89%), chippering (8%), chuck (2%), and growl (<1%). Average characters of the chip vocalization for males and females, respectively, are: maximum frequency (in kHz), 10.82, 12.25; minimum frequency (in kHz), 2.74, 2.75; terminal frequency of syllable (in kHz), 4.00, 4.04; mean frequency (in kHz), 7.19, 7.24; dominant harmonic (maximum intensity), 4.80, 4.83; syllables/call, 12.83, 12.89; call rate/min, 30.00, 30.11. Females call with higher maximum frequency than males. There are no significant differences between sexes for other parameters (Gannon and Stanley, 1991). Trapped chipmunks may emit trills (Callahan, 1975).

GENETICS. Tamias palmeri has a type B karyotype. The diploid karyotype contains 38 chromosomes including four pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and three pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is acrocentric (Sutton and Nadler, 1969).

Based upon 20 allozymes, *T. palmeri* had an average heterozygosity of 0.0416 and two polymorphic loci (serum transferrin and red cell phosphoglucomutase—Levenson et al., 1985). An electrophoretic examination of blood serum proteins revealed that there were no differences between individuals of different sex, age, or period of captivity (Burgwardt, 1968).

REMARKS. Based upon phenetic analyses of morphologic characters, T. palmeri has been grouped in a cluster with T. quadrivittatus and T. umbrinus (Levenson et al., 1985), and in the same cluster as T. cinereicollis, T. dorsalis, T. panamintinus, T. quadrivittatus, and T. umbrinus (Nadler et al., 1985). Cladistic analyses of electrophoretic data placed T. palmeri with T. merriami, T. obscurus, T. sonomae, and T. townsendii (Nadler et al., 1985). Previously, T. palmeri was placed in the quadrivitatus group with T. canipes, T. cinereicollis, T. bulleri, T. durangae, T. quadrivitatus, T. ruficaudus, T. speciosus, and T. umbrinus (Howell, 1922), and in the speciosus group with T. bulleri, T. panamintinus, T. umbrinus, and T. speciosus (White, 1953). However, T. palmeri more recently has been placed in the merriami species group with T. bulleri, T. merriami, and T. obscurus (Levenson et al., 1985).

Because of indistinguishable bacula (White, 1953) and because it was not possible to distinguish T. palmeri from T. umbrinus inyoensis when body measurements, cranial measurements, and coloration were compared, Sutton (1982) and White (1953) believed that T. palmeri probably was a subspecies of T. umbrinus. Based on analyses of bacula of T. palmeri, T. quadrivittatus, and three populations of T. umbrinus, Stanley (1991:30) tentatively suggested that T. palmeri should be designated as a subspecies of T. umbrinus, although his data showed that "... the baculum of the Spring Range umbrinus [=T. palmeri] is relatively distinctive, in that it exhibited the most acute angle and greatest height of the shaft." In addition, Stanley (1991:24) found more bacular characters that differed be-

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tween T. palmeri and T. umbrinus (height of keel, height of shaft, angle between tip and shaft) than between T. quadrivittatus and T. umbrinus (length of shaft, greatest width of shaft at base); T. palmeri differed from T. quadrivittatus in length of shaft, height of keel, height of shaft, angle between tip and shaft, greatest width of shaft at base, and least width of shaft at neck. The baubellum of T. palmeri is similar to that of T. umbrinus, except that it is larger in all respects (Sutton, 1982).

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LITERATURE CITED

- ARCHIE, I. H., B. B. BABERO, AND H. N. DWYER. 1988. Some helminth parasites of chipmunks, Eutamias spp. (Sciuridae) in southern Nevada. Proceedings of the Helminthological Society of Washington, 55:74-76.
- BLACK, C. C. 1972. Holarctic evolution and dispersal of squirrels
- (Rodentia: Sciuridae). Evolutionary Biology, 6:305-322.
 BRADLEY, W. G., AND M. K. YOUSEF. 1974. Thermoregulation of chipmunks (Eutamias) as related to ecologic distribution. Proceedings of the International Union of Physiological Sciences, 11:106.
- BROADBOOKS, H. E. 1974. Tree nests of chipmunks with comments on associated behavior and ecology. Journal of Mammalogy, 55:630-639.
- BURGWARDT, L. C., JR. 1968. A comparison of certain members of the genus Eutamias by blood serum protein electrophoresis. Dissertation Abstracts, 28B:4799-4800.
- BURT, W. H. 1934. The mammals of southern Nevada. Transactions of the San Diego Society of Natural History, 7:375-
- CALLAHAN, J. R. 1975. Status of the peninsula chipmunk. Journal of Mammalogy, 56:266-269.

 Deacon, J. E., W. G. Bradley, and K. M. Larsen. 1964. Eco-
- logical distribution of the mammals of Clark Canyon, Charleston Mountains, Nevada. Journal of Mammalogy, 45:397-409.
- ELLIOT, D. G. 1901. A synopsis of the mammals of North America and the adjacent seas. Field Columbian Museum Publications, Zoölogical Series, 2:1-522.
- ELLIS, L. S., AND L. R. MAXSON. 1979. Evolution of the chipmunk genera Eutamias and Tamias. Journal of Mammalogy, 60: 331-334.
- GANNON, W. L., AND W. T. STANLEY. 1991. Chip vocalization of Palmer's chipmunk (Tamias palmeri). The Southwestern Naturalist, 36:315-317.
- HAFNER, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3-23, in The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.
- HALL, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, 710 pp.
- 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1-600 + 90. HIRSHFELD, J. R. 1975. Reproduction, growth, and development
- of two species of chipmunks: Eutamias panamintinus and

Eutamias palmeri. M.S. thesis, University of Nevada, Las Vegas, 84 pp.

5

- HIRSHFELD, J. R., AND W. G. BRADLEY. 1976. Oxygen consumption and development of thermoregulation in young Eutamias panamintinus and Eutamias palmeri. Comparative Biochemistry and Physiology, A. Comparative Physiology, 55:89-90.
- -. 1977. Growth and development of two species of chipmunks: Eutamias panamintinus and E. palmeri. Journal of Mammalogy, 58:44-52.
- HOFFMANN, R. S. 1981. Different voles for different holes: environmental restrictions on refugial survival of mammals. Pp. 25-45, in Evolution today (G. G. E. Scudder and J. L. Reveal, eds.). Proceedings of the Second International Congress of Systematic and Evolutionary Biology, Hunts Institute for Botanical Documentation, Carnegie-Mellon University, Pitts-

burgh, Pennsylvania, 486 pp.
HOFFMEISTER, D. F. 1986. Mammals of Arizona. The University of Arizona Press and The Arizona Game and Fish Department

- [Tucson], 602 pp. Honacki, J. H., K. E. Kinman, and J. W. Koeppl (eds.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.
- HOWELL, A. H. 1922. Diagnoses of seven new chipmunks of the genus Eutamias with a list of the American species. Journal of Mammalogy, 3:178-185.
- 1929. Revision of the American chipmunks (genera Tamias and Eutamias). North American Fauna, 52:1-157.
- HUBBARD, C. A. 1949. Fleas of the state of Nevada. Bulletin of the Southern California Academy of Sciences, 48:115-128.
- JAEGER, E. C. 1955. A source-book of biological names and terms. Third ed. Charles C Thomas Publisher, Springerfield, Illinois,
- LEVENSON, H. 1979. Sciurid growth rates: some corrections and additions. Journal of Mammalogy, 60:232-235.
- 1990. Sexual size dimorphism in chipmunks. Journal of Mammalogy, 71:161-170.
- LEVENSON, H., R. S. HOFFMANN, C. F. NADLER, L. DEUTSCH, AND S. D. FREEMAN. 1985. Systematics of the Holarctic chipmunks (Tamias). Journal of Mammalogy, 66:219-242.
- MERRIAM, C. H. 1897. Notes on the chipmunks of the genus Eutamias occurring west of the east base of the Cascade-Sierra system, with descriptions of new forms. Proceedings of the Biological Society of Washington, 11:189-212.
- MILLER, G. S., JR. 1924. List of North American Recent mammals 1923. Bulletin of the United States National Museum, 128: 1 - 673.
- NADLER, C. F., R. S. HOFFMANN, AND D. M. LAY. 1969. Chromosomes of the Asian chipmunk Eutamias sibiricus Laxmann (Rodentia: Sciuridae). Experientia, 25:868-869.
- NADLER, C. F., R. S. HOFFMANN, AND H. LEVENSON. 1985. Biochemical and morphological relationships among Holarctic chipmunks. Acta Zoologica Fennica, 170:19-23.
- NADLER, C. F., R. S. HOFFMANN, J. H. HONACKI, AND D. POZIN. 1977. Chromosomal evolution in chipmunks, with special emphasis on A and B karyotypes of the subgenus Neotamias. The American Midland Naturalist, 98:343-353.
- O'FARRELL, T. P. 1980. Eutamias growth rates: additional corrections. Journal of Mammalogy, 61:364-366.
- PATTERSON, B. D. 1984. Geographic variation and taxonomy of Colorado and Hopi chipmunks (genus Eutamias). Journal of Mammalogy, 65:442-456.
- RIDGWAY, R. 1912. Color standards and color nomenclature. R.
- Ridgway, Washington, D.C., 340 pp.
 Scott, I. M., M. K. Yousef, and W. G. Bradley. 1972. Body fat content and metabolic rate of rodents: desert and mountain. Proceedings of the Society for Experimental Biology and Medicine, 141:818-821.
- Scott, I. M., M. K. Yousef, and H. D. Johnson. 1976. Plasma thyroxine levels of mammals: desert and mountain. Life Sciences, 19:807-812.
- STANLEY, W. T. 1991. An analysis of the biogeographic relationships of four populations of the Uinta chipmunk (Eutamias umbrinus) using phallic morphology. M.A. thesis, Humboldt State University, Arcata, California, 41 pp.
- SUTTON, D. A. 1982. The female genital bone of chipmunks, genus Eutamias. The Southwestern Naturalist, 27:393-402.

SUTTON, D. A., AND C. F. NADLER. 1969. Chromosomes of the North American chipmunk genus *Eutamias*. Journal of Mammalogy, 50:524-535.

WHITE, J. A. 1953. The baculum in the chipmunks of western
North America. University of Kansas Publications, Museum
of Natural History, 5:611-631.

Yousef, M. K., H. D. Johnson, W. G. Bradley, and S. M. Seif. 1974. Tritiated water-turnover rate in rodents: desert and mountain. Physiological Zoölogy, 47:153-162.

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LITERATURE CITED

- ARCHIE, I. H., B. B. BABERO, AND H. N. DWYER. 1988. Some helminth parasites of chipmunks, Eutamias spp. (Sciuridae) in southern Nevada. Proceedings of the Helminthological Society of Washington, 55:74-76.
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- (Rodentia: Sciuridae). Evolutionary Biology, 6:305-322.
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- BROADBOOKS, H. E. 1974. Tree nests of chipmunks with comments on associated behavior and ecology. Journal of Mammalogy, 55:630-639.
- BURGWARDT, L. C., JR. 1968. A comparison of certain members of the genus Eutamias by blood serum protein electrophoresis. Dissertation Abstracts, 28B:4799-4800.
- BURT, W. H. 1934. The mammals of southern Nevada. Transactions of the San Diego Society of Natural History, 7:375-
- CALLAHAN, J. R. 1975. Status of the peninsula chipmunk. Journal of Mammalogy, 56:266-269.
- DEACON, J. E., W. G. BRADLEY, AND K. M. LARSEN. 1964. Ecological distribution of the mammals of Clark Canyon, Charleston Mountains, Nevada. Journal of Mammalogy, 45:397-409.
- ELLIOT, D. G. 1901. A synopsis of the mammals of North America and the adjacent seas. Field Columbian Museum Publications, Zoölogical Series, 2:1-522.
- ELLIS, L. S., AND L. R. MAXSON. 1979. Evolution of the chipmunk genera Eutamias and Tamias. Journal of Mammalogy, 60:
- GANNON, W. L., AND W. T. STANLEY. 1991. Chip vocalization of Palmer's chipmunk (Tamias palmeri). The Southwestern Naturalist, 36:315-317.
- HAFNER, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3-23, in The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.
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- 1977. Growth and development of two species of chipmunks: Eutamias panamintinus and E. palmeri. Journal of Mammalogy, 58:44-52.
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- [Tucson], 602 pp. Honacki, J. H., K. E. Kinman, and J. W. Koeppl (eds.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.
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 —. 1929. Revision of the American chipmunks (genera
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- HUBBARD, C. A. 1949. Fleas of the state of Nevada. Bulletin of the Southern California Academy of Sciences, 48:115-128.
- JAEGER, E. C. 1955. A source-book of biological names and terms. Third ed. Charles C Thomas Publisher, Springerfield, Illinois, 323 pp.
- LEVENSON, H. 1979. Sciurid growth rates: some corrections and additions. Journal of Mammalogy, 60:232-235.
- . 1990. Sexual size dimorphism in chipmunks. Journal of Mammalogy, 71:161-170.
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- MILLER, G. S., JR. 1924. List of North American Recent mammals 1923. Bulletin of the United States National Museum, 128: 1-673.
- NADLER, C. F., R. S. HOFFMANN, AND D. M. LAY. 1969. Chromosomes of the Asian chipmunk Eutamias sibiricus Laxmann (Rodentia: Sciuridae). Experientia, 25:868-869.
- NADLER, C. F., R. S. HOFFMANN, AND H. LEVENSON. 1985. Biochemical and morphological relationships among Holarctic chipmunks. Acta Zoologica Fennica, 170:19-23.
- NADLER, C. F., R. S. HOFFMANN, J. H. HONACKI, AND D. POZIN. 1977. Chromosomal evolution in chipmunks, with special emphasis on A and B karyotypes of the subgenus Neotamias. The American Midland Naturalist, 98:343-353.
- O'FARRELL, T. P. 1980. Eutamias growth rates: additional corrections. Journal of Mammalogy, 61:364-366.
- PATTERSON, B. D. 1984. Geographic variation and taxonomy of Colorado and Hopi chipmunks (genus Eutamias). Journal of Mammalogy, 65:442-456.
- RIDGWAY, R. 1912. Color standards and color nomenclature. R.
- Ridgway, Washington, D.C., 340 pp.
 Scott, I. M., M. K. Yousef, and W. G. Bradley. 1972. Body fat content and metabolic rate of rodents: desert and mountain. Proceedings of the Society for Experimental Biology and Medicine, 141:818-821.
- SCOTT, I. M., M. K. YOUSEF, AND H. D. JOHNSON. 1976. Plasma thyroxine levels of mammals; desert and mountain. Life Sciences, 19:807~812.
- STANLEY, W. T. 1991. An analysis of the biogeographic relationships of four populations of the Uinta chipmunk (Eutamias umbrinus) using phallic morphology. M.A. thesis, Humboldt State University, Arcata, California, 41 pp.
- SUTTON, D. A. 1982. The female genital bone of chipmunks, genus Eutamias. The Southwestern Naturalist, 27:393-402.

SUTTON, D. A., AND C. F. NADLER. 1969. Chromosomes of the North American chipmunk genus *Eutamias*. Journal of Mammalogy, 50:524-535.

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